THE DISTRIBUTION OF PLANTS.

BY V. M. SPALDING.

AN unusual degree of interest has recently been manifested, both in the general subject of the geographical distribution of plants, and in the special study of areas occupied by natural groups, with reference to questions of relationship. In view of this interest, indicated in part by various important papers and monographs that have lately appeared, it may be that an outline of the historical development of the subject, and the present condition of our knowledge in regard to it, may serve a timely purpose.

The history of the philosophical study of geographical distribution properly begins, with the opening of the present century, with the classical essay of Alexander von Humboldt on the "Geography of Plants."[1] Fifty years before that time Linnæus[2] had discussed the habitats of plants, with reference to the physical conditions by which they appeared to be determined, and somewhat later had considered the dissemination of seeds by winds and other agencies, and the influence of climate and latitude; but Humboldt was the first to approach this study with the distinctively scientific spirit that subordinates facts to principles, and endeavors to give to all observed phenomena a rational explanation.

Humboldt's habits of study led him to think of the vegetation of the earth from the standpoint of the physical geographer rather than that of the biologist. In the "Ansichten der Natur," published in its final form many years later, the prominence still given to physical conditions, and the fixed habit of deriving conclusions from numerical data, furnish a striking comment

[1] Essai sur la Géographie des Plantes, 1805.

[2] For a brief and discriminating reference to the writings of Linnæus upon the subject, and the still earlier observations of Tournefort, see the address of Sir J. D. Hooker before the Geographical Section of the British Association at the York meeting, 1881, where other important references may also be found.

upon the hopefulness of attaining correct biological conceptions through strictly mathematical processes. He laid down the principle that "the predominance of certain families of plants determines the character of a landscape, and whether the aspect of the country is desolate or luxuriant, or smiling and majestic;" and further, that "the predominance of a particular species, as to the number of individuals,—the mass,—or, on the other hand, the lack of certain species, may give to a region a peculiar physiognomy." Connecting his thought, in the usual way, with man and his welfare, he says: "Grasses forming extended savannahs, or the abundance of fruit-yielding palms, or social coniferous trees, have respectively exerted a powerful influence on the material condition, manners, and character of nations, and on the more or less rapid development of their prosperity."

From this point of view, then, the first thing to be undertaken in the study of the geography of plants was to bring out the conspicuous characteristics of the flora of a given region by determining the number of species of a particular family, as compared with the whole number of species constituting the flora of the region in question. As a single specimen of the laborious comparisons carried out by him may be cited his tabulated statements of the estimated preponderance of various families of plants in the north temperate zone.[3]

It is unnecessary to say that he did not possess, at that time, sufficient data for making such estimates more than approximate. Nor if they had been exact would they have brought out the real principles involved. Humboldt himself seems to have felt this, and to have groped almost painfully after the solution of the problem. "The forms of organic beings," he says, "are reciprocally dependent on one another. Such is the unity of nature, that these forms limit each other in obedience to laws which are probably connected with long periods of time." He anticipated,

[3] The number of species of several conspicuous families were compared with the whole number of species of that zone. Thus:

Glumaceæ, $\frac{1}{8}$.
Compositæ, $\frac{1}{8}$.
Leguminosæ, $\frac{1}{18}$.
Labiatæ, $\frac{1}{24}$.
Umbelliferæ, $\frac{1}{40}$.
Amentaceæ, $\frac{1}{45}$.
Cruciferæ, $\frac{1}{19}$.

in some measure, the results of later investigations; but even his extraordinary genius, that seemed to compass the whole earth in its giant grasp, was forced at last, baffled and eluded, to yield the question and leave the field.

Humboldt's real service, then, was not so much in developing the laws of distribution as in boldly stating the problem and showing more clearly than it had ever been shown before how much there was to be accounted for. It needs but a slight acquaintance with his writings to feel convinced that the whole subject of distribution had scarcely been worked beneath the surface; the lines had been sighted and the stakes driven, but deeper explorations were left for future workers.

The well-known treatise of Alphonse De Candolle, "The Géographie Botanique Raisonnée," [4] appeared just half a century after the publication of Humboldt's essay. It is hardly too much to say that, compared with all that had preceded it, this great work showed such an increase of knowledge, with a breadth of view and capacity for generalization, as rendered it a permanent record of the sum total that had been accomplished up to the middle of the present century in this study.

An examination of De Candolle's treatise shows that there were, at that time, clear ideas regarding the relations of plants to physical conditions; that the shape of the area occupied by a species —approximately circular or elliptical—had been noticed; and disjoined species—those occupying widely separate areas—had received a certain amount of attention; that the greater part of existing species were then, as now, held to be of high geological antiquity, although it was also held that they originated by successive creations; and finally that the relations of species to genera, families, and higher groups were beginning to be studied in the light of facts of distribution.

De Candolle had fairly done what, at this time, lay within the power of man to do. He had gathered an overwhelming array of facts, had marshalled them with orderly precision, had tried them—not wholly satisfactorily, it is true—with reference to their theoretical bearing, and had given them to the world ready to use.

[4] Paris, 1855.

But there was still needed some great fundamental conception to bind these facts together into a consistent whole; and this conception, brought out three years later in the famous papers of Wallace and Darwin before the Linnæan Society, was embodied and applied, more and more completely, in the various monographs and essays of the three botanists: Asa Gray in the United States, and J. D. Hooker and George Bentham in England.

The history of the subject now becomes so largely identical with the contributions of these three men[5] that we can do no better than to follow each one of them step by step in his work, and see, as far as we are able, the facts as they saw and interpreted them.

The botanical contributions of Asa Gray, taken as a whole for fifty years, bore more or less directly upon the subject of geographical distribution. One of his earliest reviews is a notice of Siebold's Flora Japanica,[6] in the course of which the remark is made that "the flora of Japan presents such striking analogies to that of the temperate part of North America as to render this work of more than ordinary interest to American botanists;" and again, in 1846, he takes the occasion offered in another review to say: "It is interesting to remark how many of our characteristic genera are represented in Japan, not to speak of striking analogous forms."

This remarkable fact, having once been clearly formulated, was never lost sight of, and although it seemed incapable of explanation upon any theory then held regarding the nature of species, Dr. Gray lived long enough to find the clue to its meaning, and to show the far-reaching and fundamental nature of the principle involved.

[5] All mention of such works as those of Schoua and Griesbach, however valuable for their statement of facts, has purposely been omitted. The service rendered by those who collect data exhaustively and accurately is by no means called in question, but it does not fall within the purpose of the present sketch to consider any treatises, however extended, that cannot be shown to have definitely contributed to a better comprehension of the principles in this study. For an entirely different reason, it has been thought best to omit any discussion of the well-known papers of Forbes and Darwin, although the former was called by Hooker "the reformer," and the latter "the greatest lawgiver," of the science of geographical distribution.

[6] *Am. Jour. Sci.*, Oct., 1840.

In 1856 and '57 Dr. Gray published in the *American Journal of Science* a continued article on the Statistics of the Flora of the Northern United States,[7] in which facts in line with those already indicated were brought out at much greater length, statistical comparisons being made between the numbers of orders, genera, and species indigenous to the Northern United States and those of Europe and Eastern Asia respectively; the close relationship of the floras of the two great continents again being brought out in a still more striking manner. His remarks on the theoretical bearing of these facts are of special interest from having appeared some little time before the "Origin of Species." Dr. Gray says: "As the discussion of this most difficult problem proceeds, the two antagonistic positions only appear to be tenable. . . . . The first theory is based upon the natural idea of species as consisting of kindred individuals descended from a common stock which, whether demonstrable or not as a fact, gives us a clear and distinct conception of species, and the only one we possess, The second theory, being incompatible with this conception, leaves species no objective basis in nature and seems to make even the ground of their limitation a matter of individual opinion."

Here was the essential conception of the real nature of species, —a conception that became more fixed as his studies continued, and was expressed more at length in a memoir presented to the American Academy in 1858–'59,[8] in which Dr. Gray says: "The natural supposition is that individuals of the same kind are descendants from a common stock, or have spread from a common center; and the progress of investigation, instead of eliminating this preconception from the minds of botanists, has rather confirmed it."

Without attempting to condense or reproduce further the substance of these earlier papers, it is enough to say that in them had already been clearly formulated two essential principles, viz., the genetic relationship of plants of the same and "representative" species, and repeated migrations under changed climatic

[7] *Am. Jour. Sci.*, 2d Ser., Vol. XXII. (1856), and Vol. XXIII. (1857).

[8] Memoirs Am. Acad., New Ser., Vol. VI.

conditions. His later papers[9] extend and confirm the observations recorded in these; and the fact that the accumulations and research of nearly thirty years afterwards did not change his views in any essential particular is of importance. The history of the big trees of California, of the forests of the Northern Continents, and the peculiarities and resemblance of the North American flora as compared with those of Europe and Asia, still were shown to point unmistakably to migrations from a former common, though extended, area, with subsequent modifications in accordance with the theory of descent.

Dr. Hooker covered a different ground in his study of geographical distribution. Taking up successively the Antarctic flora, and those of New Zealand, Tasmania, and the Oceanic Islands, it was only at a later period in his investigations of the floras of Southern Asia and of the Arctic regions that he overlapped in any way the ground already occupied by Dr. Gray.

His position in regard to theories then prominent was distinctly indicated in the "Introductory Essay to the Flora of Tasmania."[10] Referring to the flora of New Zealand,[11] in which he had given (though without distinctly endorsing) the prevalent view, that species are created as such, he says: "In the present essay I shall advance the opposite hypothesis, that species are derivative and unstable."

Of the observed facts recorded in this series of monographs only a few of the most important can be mentioned.

It was shown in the Flora Antarctica that a certain relationship exists between floras of the Antarctic Islands and that of the ex-

[9] Three papers of Professor Gray contain his latest contributions to this subject, and represent his mature views and final judgment regarding the distribution of plants in the Northern Hemisphere. These are:

1. Sequoia and its History: The Relations of North American to Northeast Asian and to Tertiary Vegetation. A presidential address to the American Association at Dubuque, August, 1872.

2. Forest Geography and Archeology. A lecture delivered before the Harvard University Natural History Society, April, 1878.

3. Characteristics of the North American Flora. An address to the botanists of the British Association at Montreal, August, 1884.

[10] *Am. Jour. Sci.*, 1860, Vol. XXIX.

[11] Reviewed in *Am. Jour. Sci.*, 1854, Vol. XVII.

treme southern portion of the American continent, and subsequent study brought out a far greater extension of this relationship.

A further interesting observation was that the plants of the Antarctic Islands that are also natives of Tasmania, New Zealand, and South America, are almost invariably found only on the lofty mountains of those countries.

In view of these and other results, Dr. Hooker was strongly impressed with the view that existing agencies are not sufficient to account for the observed facts, and concludes that these floras "exhibit a botanical relationship as strong as that which prevails throughout the land within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes."

In the "Outlines of the Distribution of Arctic Plants," published in 1861, an attempt was made to trace the distribution of every phænogamous species known to occur spontaneously within the Arctic circle. The distinctively Scandinavian character of the Arctic flora, the remarkable deficiency of Greenland in characteristically American species, and the fact that no close relation was discovered between the isothermal lines and the amount of vegetation, so that the observed facts remained to be accounted for in some other way than by reference to present climatic conditions, were some of the most important results of this study. The explanation offered involved the two principles already established by Dr. Gray, viz., the community of origin of closely related species, and forced migrations under the influence of climatic changes.

The results of Dr. Hooker's study of insular floras were embodied in a paper presented to the British Association at its Nottingham meeting in 1866.[12] It contained the most extended account that has yet been given of island life from the strictly botanical point of view. The author emphasizes the fact that the flora of no oceanic island is independent and *sui generis*, but is always very manifestly allied to some continental flora; but that they all

[12] Translated in the *Ann. des Sci. Nat.*, Sér. V., Tom. 6.

have numerous and very remarkable species peculiar to them, and which distinguish them from the continental islands. He discusses at length the possibility of transoceanic communication, and although still impressed with the difficulty of accounting for the distribution of plants on oceanic islands by reference to agencies now in operation, he is far less inclined to deny that these may be sufficient than in his discussion of the floras of New Zealand and Tasmania. In fact, he seems ready to admit the full force of the argument, as recently stated by Wallace, for their distribution by natural agencies now acting, although there were still certain difficulties that did not seem to him to readily yield themselves to such an explanation.

Hooker's extended and long-continued study of the distribution of plants in every part of the Eastern hemisphere had led him to essentially the same conclusions as those reached by Dr. Gray. Both had come perforce to think of species as unstable, and both, while recognizing to the full extent the action of existing agencies of dispersal, had felt the necessity of assuming the action of climatic changes antedating the present geological epoch, the results of these changes being in a good degree definite and ascertainable in the Northern hemisphere, less definite and more perplexing in the Southern.

The most voluminous writer, and the one who has perhaps done the most, taken all in all, to advance our knowledge of the distribution of plants, was George Bentham, who for fifty-seven years, ending with his death in 1883, contrived to produce, one after another, floras, monographs, and other botanical papers, until even a review of them become a herculean task.

He approached the subject differently from either Gray or Hooker. Finally recognizing, equally with them, the importance of the theory of descent as an essential factor, he undertook to apply this by a laborious and exhaustive comparison of botanical characters and actual geographical location of species, genera, and sub-orders. "If," he says, "the two theories be admitted, that allied species and genera have a common origin, and that the descendants of a common stock placed in different regions having no inter-communication will vary in these different regions

with different combinations of characters, it will be seen how much geographical distribution may be made to check the value given to generic or other groups founded upon technical distinctions." In other words, he inaugurated the actual use of facts of geographical distribution as an aid to classification.[13]

The method pursued by Gray and Hooker in determining the species that occupy a given region, and comparing this region botanically with others, brings the geographical side of the question into prominence; and in the hands of botanists conversant with the principles of physical geography it has served to furnish important evidence bearing upon questions that are properly of a geological nature. Bentham's method, on the other hand, consisting in the exhaustive study of various families of plants, with the distribution of each of their species, as far as this is known, the world over, suggests greater possibilities than the former, inasmuch as it offers at least the hope of one being able some time to follow, step by step, the descendants of a common ancestor as they have spread themselves over the face of the earth. Such monographs as those of Bentham's on the Campanulaceæ[14] and Compositæ[15] are excellent specimens of what has already been accomplished in this direction, and if they are somewhat disappointing in coupling few conclusions with enormous labor, they point out none the less the way in which those who care to lay solid foundations for future studies of this kind will probably choose to work.

Thus far it has been attempted rather to indicate the successive steps that have been taken in this line of investigation since the time it became a subject of scientific inquiry, rather than to discuss results and theories. If, now, a brief summary of the present status as a whole is made, it appears, in the first place, that the observed facts relating to the distribution of plants correspond in every essential respect with what has been observed of the

[13] The results of Bentham's studies up to 1869 are epitomized in the presidential address of that year to the Linnæan Society (translated in the *Ann. des Sci. Nat.*, Sér. V., Tom. XI.), and are summarized by Prof. W. T. Dyer in the article "Distribution;" in the Encyclopedia Britannica.

[14] *Jour. Linn. Soc.*, Vol. XIII.

[15] Ibid., Vol. XV.

geographical distribution of animals. Making allowance for the greater age of plant life and the facility with which seeds are carried over barriers not easily crossed by animals, it is plain that the same laws have governed in the one case as in the other.

In the second place, although the theory of dispersal of each species from a single centre, occupied by its own ancestral form, has been found to harmonize better with the facts thus far observed than any other, the application of this principle, simple and intelligible in itself, is beset with practical difficulties, owing to the complicated relations of the various agencies involved.

It seems perfectly plain, for example, that changes of climatic conditions have had much to do with the present distribution of plants in both hemispheres, but just how much it is hard to tell; and, in the same way, the extent to which ordinary means of dispersal, such as wind, water, etc., have operated can hardly be determined with precision.

To illustrate: when we find in Eastern Asia our own gold-thread, blue cohosh, twin-leaf and mandrake, poison ivy and prickley ash, Mayflower, snowberry, partridge-berry, and a host of other either identical or equivalent species, and find all these absent from Europe, we feel no hesitation in taking these facts in connection with the paleontological evidence in assuming that the changes of climate during the glacial epoch have been largely, we might fairly say chiefly, the physical factors involved; but when we find, to follow Hooker's enumeration, fifty and seventy-five New Zealand plants indigenous to Northern Europe, thirty-eight common to Australia, Northern Europe, and Asia, about fifty of those of Terra-del-Fuego in North America and Europe, and close relatives of other European species on the island of Fernando Po and the mountains of Abyssinia, it is by no means easy to account for it all.

Much is still required, from different sources, in order to the future advantageous study of the whole question. It is hardly necessary to say that notwithstanding the very extensive collections of plants that already exist in numerous herbaria, the first condition of the comprehensive study of any one order with reference to its distribution is the gathering of still more of its

species, particularly from regions still imperfectly known botanically, into the great herbaria where proper facilities for study and clasification are provided.

There is great need of more exact observations of actual cases of transportation of seeds to great distances. We are not yet in a position to say, with definiteness, how much can be explained in this way. Whoever records a single absolutely reliable observation of this kind will render a good service.

Climatic changes remain, and probably must still remain, the the least definite of all the factors thus far considered. From whatever source it may come, a clearer conception of the physical conditions formerly prevailing in the Southern hemisphere seems indispensable. This is, perhaps, not hopeless, but it is, to all appearances, not likely to be immediately realized.

Paleontological evidence has been slowly accumulated, enough to show how much need there is of more. Species now perfectly isolated, living in tropical America on the one hand, and in Southern Asia on the other, have had their relations cleared up by finding their ancestral forms scattered through the intervening regions; and the prosecution of this part of the study is as hopeful as it is difficult. But the successors of Heer and Lesquereux are not likely to be numerous, nor to turn out results very rapidly.

One more side of approach remains, seemingly most hopeful, perhaps really most hopeless of all; offering almost unlimited possibilities, but involving endless labor and endless complications. This is the study of single groups from a more strictly biological standpoint. Nothing but the merest beginning has yet been made. The method is illustrated in a short paper recently prepared by Prof. Huxley; more, apparently, as a piece of tentative preliminary work suggestive of what may be done than as a formal contribution.[16]

Spending a few weeks, in the summer of '86, in the mountain region near the valley of the Rhone, he began to study some of Alpine flowers, and among them the gentians. He at once experienced trouble in "analyzing" the species, which, as in so many other cases, obstinately refused to conform to the book

[16] *Jour. Linn. Soc.*, Vol. XXIV., 1888.

descriptions, and finally set out to see for himself what such an amount of variation meant.

Confining himself to the structure of the flowers, as he afterward studied the order at the Kew Gardens, he found some seven or eight modifications of its structure, arranged in two series, and presenting a complete gradation of forms, from the completely open, stellate condition, through the bell-shaped to the extreme tubular forms with which we are best acquainted in our American flora. A comparison of these various forms indicates their derivation by successive slight modifications from an original, simple flower that Professor Huxley calls the "ur-gentian," and Müller, in the "Alpenblumen," [17] does not hesitate to employ to its full extent the Darwinian theory to explain the evolution of the more highly developed and differently colored forms to the agency of insects, particularly bees and butterflies.

If this is admitted, it becomes quite as necessary to know the whereabouts and habits of bees and butterflies as to study the gentians themselves, and the interesting hint is thrown out that those gentians that have remarkably long, tubular corollas are found in such regions as Madagascar and Guiana, with their large Lepidoptera provided with a long suctorial apparatus.

Evidently a somewhat complicated set of relations has been introduced; and after still other suggestions looking in the same direction, Prof. Huxley adds to our feeling that the subject is growing in magnitude by saying: "I think there is no greater mistake than to suppose that distribution, or indeed any other large biological question, can be studied to good purpose by those who lack either the opportunity or inclination to go through what they are pleased to term the drudgery of exhaustive anatomical, embryological, and physiological preparation."

Finally he raises the significant question: "Is anybody in a position to deny that, in the absence of all other phænogamous vegetation, the gentians might have occupied every region and station on the earth's surface in which flowering plants can exist? Is there any ground for seeking the causes of this distribution elsewhere than in the competition with other plants which they

[17] Quoted by Huxley, l.c.

have undergone and are undergoing, and in the course of which it has often happened that the success of a given form in adapting itself to certain conditions has involved a corresponding diminution of the faculty of adapting itself to others? . . . From the point of view of the evolution doctrine," he adds, "it is obvious that taxonomy and distribution have to be subjected to a process of revision which will hardly fail to revolutionize both."

Manifestly the end has not yet been reached. A panorama of more than ordinary interest has been going on, larger than it is easy to imagine, and we are barely able to get a partial view of its latest phases, or, at rare intervals, to read fragments of its history. And yet it is perfectly certain that the effort to see and comprehend more of it will never be abandoned. New glimpses are obtained from time to time as the curtain is lifted a little way, and once in a while a portion of the old record comes to light and gives new hope and a new impulse.

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EDITORIAL.

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THE late meeting of the American Association for the Advancement of Science, held at Indianapolis, was a pleasant and instructive occasion. The local accommodations were of the most ample character. The sections met under the roof of the State Capitol, and the conveniences of the building were thrown open to the Association. The scientists of Indiana lent their aid to render the occasion worthy of the high place which the State holds in the Union as a centre of scientific work. The city of Indianapolis contains a large intelligent and progressive element, which has kept pace with the remarkable increase in population which the city has experienced during the last decade. This intelligence was especially reflected in the press reports of the proceedings, which were among the best that the Association has received.

Many papers of a high order of merit were read, both before the regular sessions and before the botanical, entomological, and